I.

The Cause of the Excretion of Water on the Surface of Nectaries.

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The excretion of water on the surface of plants, containing more or less solid substance in solution, is a very common phenomenon. It may be taken for granted that every one at all familiar with vegetation has observed some of these numerous cases.

Most plants when wounded in the spring present a flowing of water from the surface of the wounded part. The grape-vine bleeds for days when pruned too late in the spring. Places are often observed on the roots or trunks of trees where the water continues flowing for many days together on account of some slight wound. Large drops of a clear fluid are often found on the tips or edges of the leaves of grass early in the morning, or in the evening, when the air is nearly or quite saturated with moisture. This is generally not dew, but water which has been forced by internal pressure to the surface of the leaves. There are very many of our common plants which when observed in a moist or saturated atmosphere, during their natural period of growth, will be found to present the same phenomenon.

This excretion of water on the teeth or tips of leaves takes place oftenest through much changed stomata, called water-pores [1]; or rarely by means of the ordinary ones [2].

Tropaeolum, Colocasia, Aconitum, Fuschia globosa, Musa, Brassica, the Grasses, Tigridia pavonia, Pilularia globulifera,

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1) De Bary, Vergleichende Anatomie 1877. p. 54.

2) Moll, Untersuchung über Tropfenausscheidung und Injection bei Blättern. Overgedruckt uit de Verslagen en Mededeelingen der Koninklijke Akademie van Wetenschappen, Afdeeling Natuurkunde 2. Keeks, Deel XV. 1880.

Iris Pseudacorus, Salix and Vitis vinifera [1]) are a few of the many illustrations which might be given of plants exhibiting this phenomenon.

Also some of the Fungi, such as Pilobolus crystallinus and Mucor mucedo give fine examples of the excretion of small drops on the surface of plants. Other instances of the excretion of water are presented in the pitchers of Sarracenia and Nepenthes, on the leaves of Pinguicula, Drosera and Dionaea. Still further is to be mentioned the excretion of water on the so called nectaries, which are of so universal occurrence in the flowers, and often on the leaves of plants.

Up to the present time, with but one exception [2]) this excretion of water, i. e. the bleeding of plants, the appearance of water on the various parts of leaves, and the occurrence of the more or less sweet fluids on the surface of nectaries has been ascribed to one and the same cause, pressure from within the plant. Either the so called root-pressure, or the pressure exerted in the stem or leaf-parts, from cells or groups of cells more or less near the point of excretion have been made to explain these various phenomena [3]).

I propose in the present investigation to deal with the phenomenon of excretion which takes place on the so called nectaries.

These nectaries may be found on the petioles (Acacia lophantha), stipules (Vicia faba), or blades (Prunus laurocerasus) of leaves. In the flower, they may be on, or form a part of any of the organs, or they may be special growths for themselves. In Fritillaria they form concavities on the inner side and at the base of each of the six perianthal divisions. In Viola they are a part of two of the five stamens. In many of the Liliaceae (Ornithogalum and Agapanthus) they form a part of the pistil. Often entire organs are changed into nectaries, as in Helleborus and Eranthis, where the petals become cup-shapped nectaries. In many cases discs, or swellings (Umbelliferae, Compositae) serve this purpose. Morphologically considered there is no unity whatever in the parts which may be appropriated to this office of excretion.

We find at first in the study of the anatomy of the nectaries little more in common than in the Morphology. Some nectaries are covered with a thick cuticula while others are entirely devoid of the same; some are provided with stomata through which the excretion finds its way to the surface, while the great majority are without them. The epidermis cells are sometimes disposed in one, oftener in two layers. A comparison of many nectaries however determines several characteristics to be nearly universal.

1) Moll l. c.
2) Pfeffer, Osmotische Untersuchungen 1877. p. 232.
3) Sachs, Lehrbuch der Botanik 1874. p. 659.

The parenchyma of the nectary, the group of cells which seems to be actively concerned in the secretion, is almost invariably made up of smaller cells than that of the tissue immediately surrounding it.

The intercellular spaces are either entirely wanting or very small. The form and color of the contents of this group of cells is also generally very marked. Various proportions of glucose with nitrogenous compounds are easily shown to exist under the microscope[1]. It is easy to prove the existence of large quantities of grape sugar[2] in the parenchyma cells of the nectaries on the leaves of Prunus laurocerasus. Sugar, or starch, or both are invariably present in more or less varying quantities.

The fluid called nectar, excreted from the surface of the nectaries is usually sweet to the taste and contains in nearly all cases a large per cent. of solid substance, the larger proportion of which is sugar.

The question which I shall attempt to answer is, how this fluid or nectar finds its way to the surface of the nectary?

We may at once exclude the so called root-pressure from consideration since Unger[3] as long ago as 1844 discovered that the nectaries on the leaves of Acaçia lophantha continued to excrete after being severed from the parent plants; and as it is a well known fact that the nectaries in the flowers of Fritillaria imperialis[4] and many others secrete nectar after having been cut and placed with their stems in water.

There are however but two ways possible for this excretion to take place. Either the nectar is forced to the surface by means of active internal pressure, which is the view entertained by botanists at the present time, or it takes its place there as the result of osmotic action exerted by a fluid on the surface of the nectary.

The following considerations and experiments will offer the means of deciding the question.

If there be placed on the surface of an animal membrane distended with water, and surrounded with a saturated atmosphere, a particle of moistened sugar, or a drop from a solution of the same, a current of water will be at once generated, flowing from the interior to the exterior of the membrane.

This current takes place according to the well known laws of Osmose and needs here no explanation.

If branches from Buxus sempervirens, Ilex and Ficus elastica[5] be cut and placed in dishes containing water, and on the surfaces of some of the leaves of each, be placed small drops of a solution of sugar, salt, or gum-

1) Behrens, Die Nectarien der Blüthen. Flora 1879. p. 2.
2) For method of proof see: Pringsheims Jahrb. VIII. p. 538. 1872.
3) Unger, Flora 1844. p. 707.
4) Sachs, Physiologie der Pflanzen. 1865. p. 236.
5) Leaves from these plants have no stomata on their upper surfaces.

arabic, by means of a pipette, we shall have the same phenomenon repeated which took place with the animal membrane. Upon covering these leaves with a bell-jar to prevent evaporation and watching the result, we shall see these small drops gradually become large ones, and finally in cases where the leaves are much inclined, flow down the inclination and drop from the surfaces.

Here again a current of water is generated and flows from the interior to the exterior through the cell-walls. This experiment may be repeated with any living plant tissue whatsoever with a similar result.

Selecting a hollow on the surface of a potato, where there are no lenticells, and placing therein the sugar solution we find the same quick response to this osmotic action. The thick cuticula of the leaves selected, and the cork layer of the potato are not sufficient to prevent the active effect of this law of Osmose. In the case of the animal membrane it makes no difference what the pressure of the water from within may be, as soon as the solution which was placed on the surface is removed by washing the current ceases. The same holds true of the leaves and plant tissues of every kind.

Fritillaria imperialis.

If we examine the flowers of Fritillaria imperialis we shall find in the interior at the base of each of the perianthal divissions a large drop of fluid, filling and hanging out from a rounded concavity, the nectary. Upon shaking away these drops we find they soon return.

Let us take two similar clusters of flowers, cut from the parent plant, both with actively secreting nectaries; remove the nectar from one cluster with a pipette, being very careful not to wound the surface of the nectaries, and from the other by means of washing with a common wash-bottle, drying the nectaries thoroughly with bibulous paper after the washing. Observing now what happens after we have placed both clusters under a bell-jar, we shall see that the nectar appears more quickly, and accumulates with more rapidity in the unwashed nectaries.

If there are old flowers in the cluster the nectaries of these will probably remain dry after the first washing. But let us remove the nectar from both clusters again, the one with a pipette and the other by washing and drying as was done at first. The nectar quickly returns in those nectaries where the pipette was used; but in the washed clusters the fluid does not again reappear unless some of the flowers are very young, in which case a third washing may be required to stop all further excretion.

From the first cluster we may again and again remove the nectar with pipette, and after each removal it will reappear; more slowly however after each repetition than on the previous time.

The nectaries on which the excretion of fluid has been stopped by washing may remain under a bell-jar in the most favorable conditions for excretion, but will continue dry until the flowers wither.

Having treated a cluster to washing until there is no further excretion, let us on a part of the nectaries place small particles of moistened sugar, on others minute drops of sugar-sirup, and still others we will leave unprovided with either. We will so arrange it that in some flowers there are nectaries provided with sugar or sirup and others with nothing on their surfaces. Retaining these flowers under a bell-jar and observing what happens we shall soon see the fluid on the surface of those nectaries provided with sugar or sirup slowly returning. In the course of two or three hours these nectaries will have their natural appearance, each being provided with its large drop of clear fluid hanging out from the concave nectary. But the nectaries in the same flowers, where sugar or sirup was not applied, remain dry and unchanged.

As a still further test a few of the nectaries on which the excretion has been induced with sugar may be again washed. Once or twice suffices to stop all excretion.

When these nectaries secrete no looger, i. e. after the washing, we may once more add sugar or sirup, which again as readily as at first, induces the excretion. which continues as though not before interrupted. By these experiments it will be seen that the flow of nectar can be wholly controlled by external treatment.

The relation existing here between the induced water current on the animal membrane or leaves, and the excretion of the nectaries of Fritillaria imperialis will readily be observed. In both cases the current from the interior to the exterior is the result of Osmose, caused by the existence of a solution on the surface of the membrane or nectary of a different quality from that existing in the interior.

How this fluid takes its place on the surface of the nectary is not wholly clear in all cases.

On many nectaries the upper layers of the walls of the epidermis-cells become disorganized; a fluid resulting from this metamorphosis raises, and finally bursts the overlying cuticula, and gives the first impetus through osmotic action to the current which flows from the parenchyma of the nectary to its surface.

On the glandular hairs of Primula sinensis[1]), Cistus creticus, Pogostemon Patschouli and many others, we have analogous examples of a fluid produced between the cell-walls and the cuticula. The same phenomenon has been observed in the excretion of gums, resins and viscid substances which are often found on the surface of buds, serving for their winter pro-

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1) De Bary, Vergleichende Anatomie, 1877. p. 95.

lection[1]. It is possible also that this fluid may sometimes take its place on the surface of the nectary in the form of an excretion. Just below the base of the leaf, on the petioles of Prunus avium are two, sometimes more nectaries in the form of small wart-like swellings[2]. On these nectaries as well as on those of Clerodendron fragrans the production of a fluid between the cuticula and the underlying cell-walls, and the gradual raising of the former, can be easily studied. Sometimes the cuticula after having been once burst assunder may be renewed by the growing of a new layer, and thus this process repeated. This may occur several times on the nectaries of Prunus laurocerasus. On those of Acacia lophanta the different conditions of the cuticula, sometimes smooth and glossy as in the youngest nectaries, sometimes raised up in one or more hillocks or swellings in those nearing a condition of excretion, and sometimes the rough edges of the cuticula, in cases where it has been already burst in active nectaries, can readily be observed with the naked eye.

In all those cases where the nectary possesses a cuticula it is burst in this way, the nectar in no instance passing through it. In others where the nectary is devoid of a cuticula the production of a fluid on the surface which starts the excretion needs further study.

Acer pseudoplatanus.

Acer pseudoplatanus offers an illustration where the excretion takes place through numerous stomata on the surface of the disc-shaped nectary[3].

Upon washing and drying these nectaries two or three times I found the excretion could be as readily controlled as in the case of Fritillaria imperialis. Each stoma opens into an open space below the guard-cells. The parenchyma of the nectary is devoid of intercellular spaces. The excretion takes place through the cells which bound this space, from five to seven in number.

Prunus laurocerasus.

The nectaries on the under side of the base of the leaves of Prunus laurocerasus were treated in the same way as those of Fritillaria, and in general with the same result.

In some cases these nectaries could be made wholly inactive by three washings, even with young leaves; with others six or seven waschings were required. It is probable that in this last case a renewal of the cutic-

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1) Hanstein, Über die Organe der Harz- und Schleimabsonderung in den Laubknospen. Bot. Zeit. 1868.

2) Reinke, Pringsheim's Jahrbücher für Botanik. Band X. 1876. p. 120.

3) Caspary, De Nectariis. 1848. p. 18. Behrens, l. c. p. 59.

ula takes place which is again burst by a further metamorphosis of the cell-wall.

After the nectaries of Prunus laurocerasus had excreted constantly for seven or eight days the nectar still contained large quantities of sugar.

I found in many cases that nectaries which had been active for a number of days, from 12 to 20, lost many of their central parenchyma cells, the walls completely disapparing; and that often an opening to the surface of the nectary in one or more places was effected through the disorganization of the epidermis cells. Many of the remaining cells gradually became thin-walled. There can be little doubt here but that the tissue of the nectary was changed into sugar. This whole process is closely related to the movements from place to place of the nourishing materials, and of the chemical changes which take place in the same.

It may seem to those who are unfamiliar with the most recent investigations in Osmose, that the slight differences which often exist between the concentration of the fluids within the plant and those on the surface of the nectaries may be insufficient to cause any especial osmotic action. In the investigations of Professor Pfeffer, whose work I have previously cited, a 1,0 % solution of cane sugar exerted a pumping-force equal to a column of quicksilver 57,1 Ctm. high. A 1,0 % solution of saltpetre gave a column of 175,8 Ctm., and the same concentration of sulphate of potassium a very much higher column. These results were obtained with an artificial membrane and serve to show the osmotic power of weak solutions.

The nectars of most plants taste sweeter and appear to contain more organic substance than that of Fritillaria imperialis. From a careful analysis of the nectar taken from the flowers of this plant I found 3,8 % solid substance. The ash was almost inappreciable. The solid substance was probably nearly all sugar.

Unger[1]) gives the specific gravity of nectars taken from three species of Agave as follows:

Agave	Americana	1,05
-	geminiflora	1,09
-	lurida	1,20.

Assuming that the solid substance in these nectars consists of cane-sugar we shall have the following per cts.:

For Agave		Americana	10 %
-	-	geminiflora	18 %
-	-	lurida	41,66 %.

Unger also gives the per cts. of sugar contained in the sap of several

1) Unger, Beiträge zur Physiologie der Pflanzen. Sitzungsberichte der Mathem.-Naturw. Classe der Kais. Academie der Wissenschaften. Bd. XXV. Juliheft 1857. p. 446.

species of maples and other trees richest in saccharine substances. In the birch he found 1,3 % sugar. The maples gave less. Schroeder [1]) found for the highest per ct. of sugar in the sap of the birch 1,92, lowest 0,34 %. With the maple the maximum reached 3,71 %, minimum 1,15 % per ct.

According to Unger the sap taken from a bleeding grape-vine on the eighth of April gave a specific gravity of 1,0009 and showed 0,07 % of sugar. Sap taken from another vine gave a sp. gr. of only 1,0001, containing almost no solid substance. This is sufficient to show the difference existing in general between the sap and nectars of plants.

It must be remembered also that the nectars often become very concentrated through the evaporation of water.

In many cases the sirup becomes so thick that sugar crystalizes out [2]).

Water Supply and its Relation to the Excretion of Nectar.

The bleeding of plants in the spring and the appearance of water on the leaves of may species, resulting from internal pressure arising in stem and root, exists in very close relations to the evaporation from the leaves and other rapidly growing parts.

The bleeding decreases as the buds are developed, and generally ceases entirely either before, or when the leaves are well unfolded and the amount of evaporation becomes great. This excretion of water on the leaves is seldom seen except in a very moist or altogether saturated atmosphere, when the cells become fully turgescent and the water is finally forced out at the stomata or water pores on the teeth or tips of the leaves.

If the condition of the atmosphere becomes drier, the evaporation from the leaves increases, and the excretion of the water from the water-pores ceases just as soon as the amount of water taken up by the roots falls below that passing off from the surface of the plant by evaporation.

The excretion from the nectary bears no such direct relation to the water supply of the plant or to evaporation from the leaves. The nectaries may be active when the water supply falls far below the necessary amount for the normal growth of the plant; even after the cells of stem and leaves loose their accustomed turgescence and become wilted. The nectaries on the leaves of Prunus laurocerasus, on a branch which was placed on a table without water in the dry air of an ordinary room, after having been kept under a bell-jar until the nectaries were active, continued to excrete nectar until the whole branch had lost more than one fourth of its weight.

The excretion of water in the bleeding of plants and on the leaves is the result of an internal pressure. The water flows out at the wound or

1) Schroeder, Die landwirthschaftlichen Versuchsstationen. Band XIV. 1871. p. 168.

2) Kurr, Untersuchungen über die Bedeutung der Nectarien in den Blumen. 1832. p. 108.

water-pore where it finds the least resistance. Such excretion can only take place when the whole mass of plant tissue is in a state of turgescence. On the other hand the excretion of water by the nectary depends upon the osmotic action of a fluid on its surface. Whether this fluid on the surface of the nectary has more or less osmotic power than the contents of the cells acted upon, or whether the cells are wholly or only in a partial state of turgescence will effect the excretion only in its rapidity. The required conditions for this one-sided water current exist when the cells are filled with a solution capable of generating more or less pressure, and their outer walls are penetrated with a fluid of a different quality from that permeating the inner and opposite walls.

The moment the entire wall of any given cell becomes saturated with a fluid of like quality, that moment all one-sided water flowing stops so far as caused by its own activity.

Neither the concentration of the nectar on the surface of the cells, nor that of the fluids filling the same, can offer any rules with reference to the excretion, unless we take into account the permeability of the cell-walls and the fluids which surround them.

Relation of Pressure to the Excretion of Nectar.

The excretion of water on the margins, teeth and tips of leaves of many plants, can at any time be reproduced by placing the given plants, after having cut them from the parent stem, under pressure [1]).

The excretion of the nectar cannot be reproduced in this way. Many nectaries on a branch of Prunus laurocerasus, which had been washed until they remained dry, were subjected to a pressure of a column of mercury 45 Ctm. in height. They remained under this pressure 24 hours, covered with a bell-jar, and in a saturated atmosphere without showing any moisture on their surfaces.

The water was forced into the leaves injecting the intercellular spaces, and flowing out in drops on wounded places. I have repeated this experiment on several plants. The result has been always the same, even with Acer pseudoplatanus, where the nectar finds its way to the surface through stomata. These stomata open however into a single wide space which has no connection whatever with the intercellular spaces of the leaf. It is readily seen from the above that water filtrates with little or no read-

1) The appearance of small drops of water on the tips and teeth of the leaves of many plants in a moist atmosphere is by no means wholly due to the so called root-pressure. The tissues of the stem may share in producing this effect. By taking thrifty plants of Impatiens glandulifera and cutting the stems off under water, and then placing the severed plant under a bell-jar in a moist atmosphere, many small drops will appear on the teeth of the leaves; occasionally large ones. This is also true with I. parviflora and Fuchsia. — Moll l. c.

iness into the tissues of the nectary. The smallness of the cells, favoring a high pressure, and the almost total failure of intercellular spaces will, in a measure, account for this.

As still further illustrating this principle I selected three branches from Prunus laurocerasus, as nearly equal in age and appearance as possible, and placed them under a bell-jar until all the nectaries were active. I now subjected one of the branches to a pressure equal to a column of mercury 25 ctm. in height, another to a negative pressure of 15 ctm., and the third I placed in a glass of water. The three branches were now covered by one and the same bell-jar.

The amount of nectar excreted was carefully observed. If there was a difference, which is quite probable, it was so slight that it was impossible to observe it without more accurate methods of measurement, than were applied. The surface of an actively secreting nectary generally differs from other surface parts of the leaf in being devoid of cuticula. Other things being equal, this should allow a more ready exit of water under pressure.

A pressure of 20 or 25 ctm. quicksilver is sufficient to inject the leaves, but may be less by an atmosphere than that existing in the small-celled tissue of the nectary.

The excretion of nectar in the case of Prunus laurocerasus has been shown not to be in direct relation to the water supply of the plant. The beginning of the excretion however, i. e. the metamorphosis of the cell-wall and the raising and final bursting of the cuticula, shows a much closer connection with the same.

Six branches from Prunus laurocerasus, all with inactive nectaries, as near alike in age and appearance as it was possible to select, were cut from the tree and placed under the following conditions:

No. 1. Subjected to a pressure of 20 ctm. quicksilver.

No. 2. Subjected to a pressure of 10 ctm. quicksilver.

No. 3. Placed in a glass of water.

No. 4. Subjected to a negative pressure of 10 ctm. quicksilver.

No. 5. End of the branch wrapped in bibulous paper, a strip of which hung down into water below.

No. 6. Placed in a glass without water. All the branches were covered with bell-jars and kept in a very moist atmosphere.

The nectaries on branch No. 1 began to excrete first after 24 hours, those on No. 2, 12 hours later, No. 3 about 13 hours after No. 2, No. 4 a few hours after No. 3, No. 5 were much slower, and only four nectaries had begun to secrete on the seventh day.

Some of the nectaries of No. 6 became moist but no further change took place and the branches gradually withered. The amount of moisture

supplied, thus seems to have a comparatively direct influence on the production of the fluid on the surface of the nectary.

I have observed that the nectaries on plants of Vicia faba and Acacia lophanta growing in pots are prevented from excreting when kept somewhat drier than the natural condition.

Influence of Temperature on the Excretion of Nectar.

The influence of temperature within certain limits on the excretion of nectar, after the nectaries have begun to be active, is not very striking.

If we select six potatoes, cut off their opposites ends, on one end of each make a round smooth hole 1 ctm. deep and 1/2 ctm. in diameter, place these in two plates three in each with a little water, supply all the six holes by means of a pipette with two small drops of a 20 % sugar solution, place one plate in a room having a temperature of 20° C. and the other in a room with a temperature of 1° C. we shall be provided with the means in these artificial nectaries of observing the influence of temperature on osmotic action[1]. If the sinking of the temperature is sufficient to produce enlargement of the minute spaces between the particles making up the plasma-membrane, thus allowing the solution in the cells through exosmose to pass out, we may have a lessening of the activity; otherwise not. The holes made in the potatoes will in both rooms in a few hours be filled with fluid, pumped up from the underlying tissues. There will be very little observable difference in favor of the warm room.

Branches of Prunus laurocerasus changed from a temperature of 18° to 20° C., under the influence of which the nectaries were very active, to a temperature of from 1° to 5° C. continued to excrete nectar for several days only a little less in amount than in the warm room. Vicia faba and Acacia lophanta were subjected to the same changes of temperature, and in the main, with similar results.

In so far as temperature is concerned, a complete analogy seems to exist between the action of these artificial nectaries, from potatoes, and of the real nectaries of plants. In Professor Pfeffer's critical study of Osmose, already cited, it has been shown that the pressure which any given solution and membrane are capable of generating is not influenced to any great extent by a change of from 15° to 20° C. The membranes used are not wholly analogous to the plasma-membrane which lines the cell-walls.

Branches of Prunus laurocerasus placed at once in a cold room before the nectaries had begun to excrete remained in a temperature for 13 days ranging from 2,5°—7° C. The nectaries showed no signs of excretion.

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1) The plate and potatoes used to test the low temperature should be placed several hours before use in the cold room, that the proper temperature at the beginning of the experiment may be secured.

During the next 14 days the thermometer rose gradually to 13,2° C. at which temperature many of the nectaries began to excrete nectar. A temperature of at least 12° C. is required in the case of Prunus laurocerasus for the metamorphosis of the cell-walls and the raising of the cuticula. After this stage has passed in the activity of the nectary a much lower temperature will suffice for the continued excretion.

Effect of Light on the Excretion of Nectar.

I placed cut flowers from Fritillaria imperialis and Helleborus purpurascens, before the buds were open, in a dark room. The flowers opened and secreted nectar as freely as those kept in the light.

Branches from P. laurocerasus, the nectaries of which were inactive were at the same time placed in a dark and a light room. The temperature was the same in each. There was no observable difference, either in the time when the nectaries began to secrete or in the amount of the excretion.

In diffused light the excretion of nectar in the nectaries of Eranthis hiemalis was almost zero. The amount was considerably increased when the flowers were placed in the sunlight.

The nectaries on the leaves of Acacia lophantha which were secreting finely in the sun, when placed 6 meters back from south windows in diffused light stopped all excretion after from one to two days; while the nectaries on such plants as were left in the sunlight continued active. The plants used were seedlings in pots, 15 to 30 ctm. high.

The nectaries on the stipules of Vicia faba, on such plants as were grown in the sun, began to secrete nectar when the first leaf was scarcely unfolded, while plants grown five meters back from large south windows, but where the direct sunlight did not reach them, never produced nectar. The latter plants, when brought into the sunlight sometimes began to secrete nectar on the first day, and always on the second. Plants grown in total darkness formed the nectaries perfectly, but never secreted nectar until brought into the sunlight. Such wholly etiolated plants secreted actively after from two to three days standing in the sunlight.

I have repeatedly removed plants of Vicia faba from the sunlight, where the nectaries were very active, into diffused light four or five meters from the windows and invariably with the same result.

Drying the nectaries at the time of removal with bibulous paper, I have found that there was no more nectar produced. Perhaps twice in 20 repetitions two or three nectaries out of 18 or 20 have secreted nectar under such conditions. It is very probable that in cases where secretion took place the nectaries had not been fully dried. Such plants as have actively secreted nectar in the sunlight and have remained inactive in dif-

fused light, begin to secrete again after a few hours when brought back into the sunlight.

Plants of Vicia faba were cultivated in small pots until they were from six to twelve Ctms. high. At this time they showed no signs of excreting nectar. They were then placed in bell-jars so arragned that the entering air passed through a tube filled with small pieces of pumice-stone which had been previonsly soaked in a solution of caustic potash. By this means the plants were allowed to continue their growth in an atmosphere entirely free from carbonic acid. When the bell-jars were placed in the direct sunlight, the nectar was secreted as freely as though the plants had been left in the open air. Whatever changes the light may cause in the contents of the cells of the nectaries, or may exercise on the tissues of the same, causing the excretion to take place, certain it is that these changes have no direct relation to assimilation.

According to Wunschmann [1]) the secretion in the pitchers of Nepenthes takes place with much more rapidity in the sunshine than in the shade.

Darwin [2]) has observed that the nectar in the flowers of Lobelia erinus and on the nectaries of Vicia sativa is only secreted in the bright sunshine. The excretion of nectar on most nectaries however is only very indirectly under the influence of light.

Absorption of Nectar.

I have observed on the nectaries of Vicia faba large drops of nectar which afterwards entirely disappeared, and under such conditions as to leave it probable that evaporation was not the cause.

In order to determine whether the nectar under certain conditions may be absorbed into the nectary I took fine plants in pots of Vicia faba grown in the sun, whose nectaries were secreting actively and placed them in diffused light in the back of a room where my previous experience had shown me that these plants would secrete no nectar on account of want of light. Large drops were standing on the nectaries. The plants were covered with bell-jars and provided with an atmosphere saturated with moisture. On the following day some of these nectaries showed no trace of nectar. The nectaries were not even moist. On the third day still others were dry. An examination with the lense showed no signs of any residue on the surface of the nectaries. There could have been no evaporation, and the only

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1) Wunschmann, Über die Gattung Nepenthes, besonders in Rücksicht auf ihre physiologische Eigenthümlichkeit. 1872. p. 38.

2) Darwin, Die Wirkung der Kreuz- und Selbstbefruchtung im Pflanzenreich. 1877. p. 388.

possible conclusion was that the nectar had been absorbed[1]. I have repeated this several times with the same result. If one places a thin section of living plant tissue in a concentrated solution of sugar-sirup and observes the same under the microscope it will be seen that the solution passes readily through the cell-walls, acts osmotically on the plasma-membrane withdrawing some of the water which the cells contain and causing a more or less rapid shrinking or contraction of this living membrane. It cannot be readily shown that any of the sugar passes through the plasma-membrane, but that the cell-walls offer no obstruction is evident. In the absorption of nectar it is easily conceivable that the sugar is taken up through imbibition by the cell-walls. Whether the sugar passes again into the cell, and if so in what combination must be further studied before anything definite can be said. The nectar on the surface of the nectaries of Prunus laurocerasus was removed with a pipette every day for eight successive days. On the eighth day the nectar appeared to be as rich in sugar (Fehlings test) as on the first, showing that there was a constant supply of the same[2].

The appearance of sugar on the surface of the nectary as well as its disappearance into the cell-walls is bound up with chemical changes and with the transport of nutritive and other materials in the plant. The whole subject needs further investigation.

General Conclusions.

In the case of the glandular hairs found on so many plants we have secretory organs wholly analogous to the nectaries, in so far as the method of secretion is concerned. There are nectaries also in which the secreting surface is made up of glandular hairs. This is the case with Vicia faba.

The secretion on the leaves of Dionaea results from an external irritation caused by the presence of a nitrogenous substance.

The direct excretion of the fluid on the surface of the leaves is probably caused by an active one-sided pressure in the underlying parenchyma cells.

The excretion in the case of Drosera may be more or less influenced in the same way by nitrogenous substances, and also in addition be partially caused by osmotic action. The excretion of water in the pitchers of Nepenthes and Sarracenia, and on the leaves of Pinguicula requires further study.

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1) Bonnier, Les Nectaires. Étude critique, anatomique et physiologique. Annales des Sciences naturelles — Botanique — VI Series. Tome VIII. 1879. — The views put forth by Bonnier with reference to the absorption of Nectar seem to me to be erroneous.

2) I have already described the metamorphosis of the parenchyma and parts of the epidermis into sugar which I observed in these nectaries.

The phenomenon which occurs under the name of honey-dew [1]) (when not connected with insects) very likely owes its origin to a process more or less closely related to the excretion of nectar.

The small drops of water which are found on the mycelium of Pilobolus crystallinus [2]) and which have been supposed to originate from internal pressure, are in all probability the result of osmotic action on the surface of the same.

If the delicate plants are allowed to stand for a short time in a dry atmosphere, the drops vanish and in the place of each will be found a group of radiating crystals, easily seen with the naked eye. If the same plant be now covered with a bell-jar many of the drops of water will reappear, and precisely in those places where the crystalls were.

If howewer the mycelium, instead of being subjected to a dry air, be very carefully washed with the most delicate brush and distilled water, and then placed in moist air under a bell-jar the drops will not as a rule quickly reappear; often not at all.

Placing very minute particles of sugar on the washed mycelium quickly produced large drops.

In a number of cases I have observed the appearance of drops on mycelium which where not turgescent, and therefore not in a condition to exert any internal pressure.

Results.

I. The excretion of nectar is caused by the osmotic action of a fluid on the surface of the nectary.
II. This has its proof in the fact that the excretion is wholly under the control of external manipulation.
III. The excretion on the surface of nectaries can be wholly stopped by washing this fluid away with water.
IV. Nectaries made inactive through the removal of this fluid by washing, can again be brought into a state of activity upon the application of a solution of similar osmotic character (sugar-solution).
V. The excretion of nectar may take place when the tissues of the plant are not turgescent.
VI. The excretion of nectar is only very indirectly effected by positive or negative pressure.
VII. The nectaries of many plants secrete equally well in light or in darkness, while those of others require either the direct sunlight or strong diffused light.
VIII. The method of excreting in the nectaries is analogous to that of the glandular hairs on may plants.

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1) Unger, Beiträge zur Physiologie der Pflanzen. Sitzungsberichte der Mathem.-Naturw. Classe der Kais. Akademie der Wissenschaften. Bd. XXV. Julihefte 1857. p. 450.

2) Sachs, Experimental-Physiologie. 1865. p. 237.

Experimental Part.

Arresting of the Secretion of Nectar by Washing, on the Nectaries of Fritillaria imperialis.

A stem of Fritillaria imperialis with three flowers, the youngest not yet open, but with nectaries just beginning to excrete, the second two thirds open, nectaries active, the third flower just fully open and nectaries filled with fluid, was taken for this experiment.

The nectaries were all washed thoroughly by means of a wash-bottle, afterwards dried with bibulous paper. It was necessary to open the bud to receive the first washing.

The nectaries of the youngest flower were washed four times, those of the other two three times during a period of three days. This was sufficient to stop all further flow of nectar. During the experiment the flowers were kept under a bell-jar in a moist atmosphere. At the end of the three days the flowers were still all fresh and young. None of the anthers were open. Such flowers, when left to their natural course of development excrete nectar for a period of from eight to ten days. When the nectar is removed with a pipette and the surface of the nectary left moist there is a quick return of the fluid. This is caused by the solution which remains on the surface and also fills the interstices of the outer cell-walls of the epidermis. It is easily understood that a constant removal of this solution with a pipette may in time so dilute the same as to stop the flow of nectar. Two causes may here be mentioned which are able to keep the nectary in a state of activity.

First: the constant evaporation of water which often reduces the nectar to a thick sirup, thus making the osmotic action much stronger than it otherwise would be; and second: the probable production for a considerable length of time in some cases, of a fluid by disorganization of the cell-walls.

In order to illustrate the difference between old and young nectaries in the continuation of the excretion, a flower from Fritillaria imperialis was selected in which the pollen was fully ripe, the anthers having already opened.

After carefully washing and drying the nectaries once the flower was placed in water under a bell-jar. The nectaries continued to remain perfectly dry.

Inducing the Excretion of Nectar on Inactive Nectaries by a Sugar-solution.

Fritillaria imperialis.

A flower stem of Fritillaria imperialis contained four flowers. The secretion on the nectaries of three was entirely stopped by washing. No excretion took place for some hours under a bell-jar in an atmosphere saturated with moisture. On some of the inactive nectaries were placed moist particles of sugar, on others a minute drop of sugar-solution, others were left in their dry condition. The nectaries supplied with sugar or sirup were, in from one to two hours filled with nectar and from this time on continued to secrete as though they had not been stopped by washing. Those nectaries left unprovided with sugar or sirup remained dry. The nectaries of one flower of the cluster were not washed and continued constantly to secrete nectar.

In the case of the flower with ripe pollen, which required but one washing to stop the excretion of the nectar, an application of a sugar solution brought all the nectaries into activity again.

Prunus laurocerasus.

On the under side, near the base of the leaves of Prunus laurocerasus are generally to be found four nectaries, two on either side of the midrib. Two branches, each with six or more leaves, the nectaries of which were active, were selected. The nectaries were washed with wash-bottle and dried with bibulous paper once each day until no further secretion appeared. Some of the nectaries required but two washings, others three, and still others as many as six repetitions. Some very young leaves required four washings. On some of these nectaries, after they had been dry and inactive during three days, were placed minute particles of moist sugar. On the following day large drops of nectar stood on these nectaries, which from this time on continued to excrete as though they had not been washed. With nectaries on which the excretion had been induced by sugar one washing was generally sufficient to again stop its flow. When bibulous paper was used for removing the nectar, a greater number of repetitions was required before the nectaries remained dry.

Eranthis hiemalis.

The tubular nectaries of seven flowers were washed and then dried with bibulous paper. On the following day this was repeated. The flowers remained under a bell-jar for several days until they withered, without further excretion of nectar.

Helleborus purpurascens.

The cup-shapped nectaries of two flowers washed and dried. After the second washing no more nectar appeared. Minute drops of a sugar-solution were placed in a few of the nectaries. Secretion again appeared in two or three hours and continued two days until the nectaries fell from the flowers. The nectaries not provided with sirup remained dry.

In the case of some of the Helleborus species I have found flowers in which the washing of the nectaries seemed not to have the slightest effect on the secretion of the nectar. Some of the nectaries were as active after eight and nine washings, applied during a period of six days, as at first.

Acacia lophanta.

Plant two feet high with 25 to 30 leaves. Placed under a bell-jar. Four nectaries on the petioles of the leaves washed and then dried. Three secreted no more nectar, the fourth required a second washing.

After two days of the most favorable surroundings, during which time these nectaries remained dry, sugar-sirup was applied to them. In a few hours the secretion accumulated and seemed to be going on normally. On the following day these nectaries were again washed. The youngest leaf again required the second manipulation before the flow of nectar ceased. After waiting one day in order to be sure that these nectaries did not again secrete, the same method of applying sirup, inducing the excretion, and again stopping it by washing, was for the third time repeated, and with similar results.

This treatment was applied to many other leaves on the same plant. Not a single nectary was observed to begin its secretion for a second time after it had once been left dry by washing. With very young plants the nectaries on the unfolding and rapidly growing leaves often required from three to five washings to effect a total stoppage of the nectar.

Acer pseudoplatanus.

Several branches placed under a bell-jar. Nectar secreted very freely, flowing in large drops over the discs and standing on the surface of the perianth.

Flowers in which the pollen was ripe required but one washing to stop the flow of nectar. Younger flowers required from two to four, according to their age. The application of a minute drop of sirup readily recalled the excretion.

Inactive Nectaries Placed under Pressure in order to See if This Would again Induce the Excretion.

Fritillaria imperialis.

Inflorescence with four flowers. The excretion of nectar in three flowers entirely stopped by washing. The flowers still young, none of the anthers having shed their pollen. This entire stem subjected to a pressure first of 20 ctm. quicksilver for five hours; and second to 40 ctm. quicksilver for another five hours. No change in the nectaries in either case observed. None of them became moist. The water was driven into the leaves, oozing out at wounded places and standing in pools on some of the under surfaces. The secretion in the one flower with active nectaries unchanged in quantity and apparently normal. The pressure seemed to have no perceptible influence either on the active or inactive nectaries.

Acer pseudoplatanus.

A branch of A. pseudoplatanus in the flowers of which the excretion of nectar had been stopped by washing was subjected to a pressure exerted by a column of quicksilver 45 ctm. high for more than 24 hours. No effect was observed on the dry nectaries. The water was driven to the surface of the delicate stems and young leaves, standing here and there in small drops. A similar trial with P. laurocerasus gave like results.

Excretion of Nectar under low Temperatures.

Prunus laurocerasus.

Several branches of P. laurocerasus whose nectaries were excreting finely in a room 17° to 20° C. were placed in a cold room. The nectar was removed with a pipette.

Feb. 2d. Monday 12 o'clock Ther. + 1° C.
- 3d. Tuesday 12 - - 5,5° C.
All the nectaries secreting slowly.
- 4th. Wed. 12 o'clock Ther. 5° C.
Nectaries active.
- 5th. Thursday 3 o'clock Ther. 3,5° C.
Nectaries secreting well.
- 6th. Friday 10 o'clock Ther. 1,6° C.
Nectaries provided with large drops of nectar.

Vicia faba.

Plants ith only the first leaf partially unfolded, four to six inches high, grown in small pots. Nectaries secrete first on the lowest pair of stipules, then on the stipules of younger leaves above.

Tuesday Feb. 10th.

Plants placed in a cold room where the Ther. stood 2,5° C. 12 o'clock.

Feb. 11th. Ther. 3,5° C. 12 o'clock.

Many nectaries secreting finely,

Nectar removed from the nectaries with bibulous paper.

Feb. 12th. Ther. 3,8° C. 9 o'clock A. M.

The nectaries from which the nectar was taken away on the previous day covered with fluid.

Feb. 13th. Ther. 3,5° C. 9 o'clock A. M.

Nectaries still active.

Feb. 14th. Ther. 3,8° C. 10 o'clock A. M.

Nectaries excreting.

Feb. 15th. Ther. 4,6° C. 10 o'clock A. M.

Nectaries active.

Nectar again removed with bibulous paper.

Feb. 16th. Ther. 4,8° C. 11 o'clock A. M.

Nectaries which were dried with bibulous paper on the 15th covered with nectar again.

Feb. 17th. Ther. 5,0° C. 10 o'clock A. M.

Nectaries still active.

These plants remained in this room until the 18th of march. The nectaries were constantly active. The temperature gradually rose to 10° C.

Comparison of the Action of Nectaries in High and in Low Temperatures.

Prunus laurocerasus.

Six branches of P. laurocerasus were selected as nearly equal in age and appearance as possible. The nectaries were all inactive. Three of these branches were placed in a warm room. The thermometer varied in this room from 18° to 21°,4 C. during the several days which the experiment lasted. In the night the Ther. sank to 12° C.

Three of these branches were at the same time placed in a cold room. In this room the temperature varied very little between day and night.

Feb. 9th, on Monday the experiment began. On Wednesday 11th. the nectaries in the warm room were all actively excreting.

The following is the record of the nectaries in the cold room.

Feb. 9th. Ther. + 5,5° C. nectaries unchanged,
- 10th. - + 2,5° C. - -
- 11th. - + 3,5° C. - -
- 12th. - + 3,8° C. A few nectaries slightly moist.
- 13th. - 3,5° C. No further change.
- 14th. - 3,8° C. One nectary is excreting slowly.
- 15th. - 4,6° C. Two nectaries are excreting, a few others look moist.
- 16th. - 4,8° C. No change from yesterday.
- 17th. - 5,0° C. - - - -

From a study of the nectaries of P. laurocerasus placed in a cold room it can easily be observed that the cuticula does not become raised, as must be the case before the nectary can begin its excretion.

It is probable that the cold prevents the disorganization of the outer layers of the epidermis-cells necessary for the production of the fluid which begins the osmotic action.

Effect of Light on the Excretion of Nectar with the Nectaries of Vicia faba.

For this experiment nine pots, each containing from six to seven plants, were disposed of in the following manner. The plants were grown in the greenhouse. When the first leaf was only partially unfolded they were brought into the laboratory and used. All the plants were kept under bell-jars.

April 6th.

I. Three pots (about 19 plants) placed in south windows in the direct sunlight.

II. Three pots of plants placed six meters back from the south windows in diffused light.

III. Three pots of plants placed in a dark cupboard standing in the same room with I. and II.

I. These plants grew rapidly. On the 8th one pair of nectaries began to secrete.

The days were dark and cloudy until the 12th.

April 12th was bright and sunny and all the plants began to secrete nectar.

II. Plants grew rapidly in diffused light but never secreted nectar.

III. Plants grew rapidly until their reserve material was exhausted, but never secreted nectar. The nectaries were well formed however.

On the 12th of April the following disposal was made of the three pots of I.

The nectar was removed from all the plants in the three pots.

Pot No. 1 was left in the sunlight.

April 14th. All the nectaries excreting copiously. Nectar again removed.

– 15th. All the nectaries very active.

Pot No. 2. Placed in diffused light six meters from the windows.

April 14th. Of the seven pairs of nectaries from which the nectar was removed only one secretes nectar to day.

– 15th. None of the nectaries are secreting.

Pot. No. 3. Placed in the dark.

April 14th. Of the five pairs of nectaries from which the nectar has been removed four are moist. Nectaries again dried.

– 15th. Four pairs of nectaries dry, one pair still moist but not active.

On April 13th. One pot of plants from II. was placed in the sunlight.

April 14th. Two pairs of nectaries began to excrete nectar.

– 15th. Many of the nectaries are secreting finely to-day.

On April 13th. One pot from III. was placed in the sunlight. Plants much etiolated; color yellow to white.

April 14th. Four pairs of nectaries have begun to excrete.

– 15th. Many of the nectaries are active.

The continuation of the excretion on a few of the nectaries placed in the dark was probably an after effect of the light.

I have placed here only a very few of the many experiments which this work required. They will serve to illustrate the method employed.

Date Due
